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Trophic ecology of the European hake in the Gulf of Lions, northwestern Mediterranean Sea

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Summary: The European hake, *Merluccius merluccius*, is an important resource for Mediterranean fisheries. This study focuses on juvenile and adult hake feeding ecology in the Gulf of Lions, using information from scientific surveys carried out during two seasons and three years (2004-2006). Stomach content and stable isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) analyses were performed, and the main factors explaining variations in $\delta^{15}\text{N}$ were investigated using GLMs. In the Gulf of Lions, hake mostly fed on crustaceans and fish and a dominant piscivorous regime was reached at 15 cm total length. Pelagic fish (sardine, anchovy and small blue whiting) were the main source of prey (40%-80%) and cannibalism was low (<5%). The results confirmed that hake is an opportunistic feeder and also showed that the size and diversity of prey vary among hake size classes, probably as a result of the different spatial distribution and/or foraging migrations. The present study finally postulates that the unbalanced sex ratio (80% female against 20% male) observed at the adult stage could be related to the combination of growth pattern differences, diet and exploitation rate on the continental shelf, where the males spend a longer period of time.

Keywords: foodweb; GLM; habitat; *Merluccius merluccius*; predator-prey relationships; stable isotopes; stomach contents.

Ecología trófica de la merluza europea en el Golfo de León, Mediterráneo noroccidental

Resumen: La merluza europea, *Merluccius merluccius*, es un importante recurso para las pesquerías mediterráneas. Este estudio se centra en la ecología alimentaria de juveniles y adultos de merluza en el Golfo de León, utilizando información de campañas científicas llevadas a cabo en primavera y otoño durante tres años (2004-2006). Se realizaron análisis de contenidos estomacales e isótopos estables ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$), mientras que la identificación de los principales factores que explican las variaciones en $\delta^{15}\text{N}$ se investigaron utilizando GLMs. En el Golfo de León, la merluza se alimenta mayoritariamente de crustáceos y peces y alcanzan un régimen piscívoro dominante a los 15 cm T_L. Los peces pelágicos (sardina, anchoa y bacaladilla pequeña) constituyen el mayor porcentaje de sus presas (40-80%) y el canibalismo es bajo (<5%). Los resultados confirman que la merluza es un alimentador oportunista y también muestran que la talla y la diversidad de las presas varían entre distintas clases de talla de la merluza, probablemente como resultado de una distribución espacial diferente y/o migraciones en busca de alimento. Finalmente, este estudio postula que la proporción de sexos desequilibrada (80% de hembras frente a 20% de machos) que se observa en estado adulto podría estar relacionada con la combinación de diferentes patrones de crecimiento, dieta y tasa de explotación en la plataforma continental, donde los machos pasan un mayor período de tiempo.

Palabras clave: red trófica; GLM; hábitat; *Merluccius merluccius*; relaciones depredador-presa; isótopos estables; contenidos estomacales.

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INTRODUCTION

The Gulf of Lions (GoL) is a rather small area (~15000 km²) of the northwestern Mediterranean that supports an intensive multi-specific fishery. European hake, *Merluccius merluccius* (Linnaeus, 1758), constitutes a significant part of the commercial landings in this area, and the stock is currently overexploited. Today only juvenile and young adult hake remain on the continental shelf after decades of intensive exploitation by bottom trawling (Jadaud et al. 2014). Hake is a permanent inhabitant of the GoL and lives in a wide bathymetric range (30-800 m depth), moving between the continental shelf, the shelf break and the slope during its life cycle (Recasens et al. 1998). The species spawns mainly on the shelf-break, where longline and gillnet fisheries target the largest individuals.

The role of hake in the GoL ecosystem is still poorly understood and the baseline information on its diet remains largely unknown, although this species is considered a key predator of this area. A shift in the main prey occurs from suprabenthic crustaceans to fish in the youngest juvenile stages (Bozzano et al. 1997, Ferraton et al. 2007); spatial and temporal diet variations have only been investigated for juveniles in the GoL (Ferraton et al. 2007). Size relationships between hake and its prey remain unknown in the GoL.

The objective of the present study is to provide new, detailed information on the feeding ecology of hake in the GoL, considering temporal, spatial and ontogenetic variability. To this end, stomach content and stable isotope ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) analyses were performed on individuals of hake caught during scientific surveys carried out in the GoL. Dietary studies based on stomach contents reflect the identifiable food ingested during the sampling period depending on the digestion rates of the prey. This approach was supplemented by the stable isotope analysis of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$). These indicators give an integrative signal of the food ingested over a longer period (weeks to months). Nitrogen is classically used as an

indicator of trophic levels, as consumers are enriched in $\delta^{15}\text{N}$ relative to their food by a rather large fractionation factor (Minagawa and Wada 1984, Vander Zanden et al. 1997, Post 2002). In contrast, $\delta^{13}\text{C}$ varies little along the foodweb and is used to identify baseline carbon sources at the base of the food chain (DeNiro and Epstein 1978, Cabana and Rasmussen 1994, Vander Zanden et al. 1997). Therefore, in addition to examining hake diet from stomach contents, we also analysed variations in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to identify the main factors that could affect hake trophic ecology during its ontogeny in the GoL.

MATERIALS AND METHODS

Data acquisition

Sampling was carried out in the GoL, at four sites on the continental shelf selected from a previous work (Ferraton et al. 2007) and two new sites on the shelf-break and upper-slope (Fig. 1). Zones 2 (in front of the Rhône River) and 4 were located at 30-50 m depth, zones 1 (under the influence of the Rhône river plume) and 3 at 70-100 m, and zones 5 and 6 at 150-250 m and 250-600 m, respectively. Sampling was performed during 14 surveys carried out between 2004 and 2006. Hake (stomach and muscle), prey (muscle), water particulate organic matter (POM), phytoplankton and zooplankton were collected on the continental shelf (zones 1 to 4) during spring and autumn 2004 and 2005 by diurnal standardized operations: bottom trawl (GOC 73 trawl, Anon. 2013), suprabenthic sledge (>0.5 mm), high-flow water pump for phytoplankton (63-200 μm) and zooplankton triple nets (>200 μm). On the shelf-break (zone 5) and slope (zone 6), only hake and its main prey were collected from 2004 to 2006 by nocturnal gillnets (30-38 mm) with stretched mesh sizes. Note that no hauls were conducted in the 50-70 m and very few hauls in the 100-150 m depth ranges, because of the risk of damage to the sampling gear. Thus, the samples of hake (Fig. 2) are not representative of the

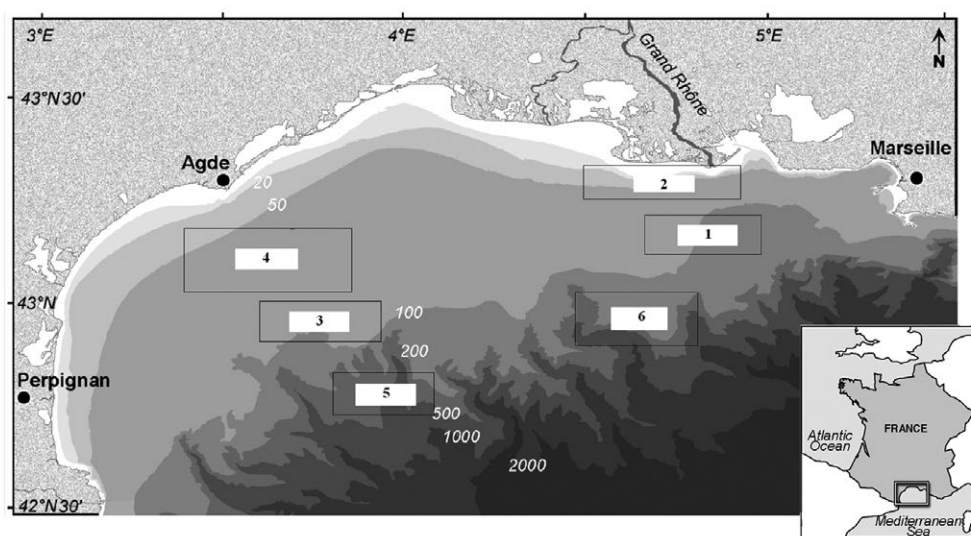


Fig. 1. – Map showing the location of sampling zones (hake and prey, 2004-2006) in the Gulf of Lions (box) in southern France.

actual spatial distribution of individuals, in particular with regard to small hakes.

To study spatial and temporal fish prey variability in stomachs, a total of 154 hauls and 20 gillnet operations were performed. Fish were measured to the nearest mm of total length (T_L) in small hakes (<25 cm) and to the nearest cm T_L for larger specimens. A total of 20 and 10 individuals per cm size class for small and large hakes, respectively, were randomly selected in each season, site and year, when available. A macroscopic maturity stage was attributed to each individual according to the gonad development. Small hakes were frozen at -20°C immediately after the catch. Large hakes were dissected on board, stomachs were removed, and both were frozen at -20°C . Hake with everted or missing stomachs, the result of necrophagic activity, were excluded from the analyses of stomach contents. Small crustaceans living in the benthic boundary water layer were collected with a suprabenthic sledge equipped with zooplankton nets (0.5 mm mesh size) (Sorbe, 1999). All fish and crustacean species susceptible to being preyed upon by hake were collected and stored frozen as a whole at -20°C . Crustaceans were sorted by large taxonomic groups (mysids, amphipods, euphausiids) and frozen at -20°C . Surface water POM was pre-filtered on 250- μm mesh sieves to remove zooplankton and large detritus, and filtered on pre-weighed Whatman GF/F filters pre-combusted for 4 h at 500°C . Phytoplankton was collected by pumping, with a submersible high-flow water pump (320 L min^{-1}), large volumes of seawater at the fluorescence maximum detected with a Seabird CTD fitted with a fluorimeter, through three different vertical nets of decreasing mesh size (200, 63 and 6 μm) (Harmelin-Vivien et al. 2008). The term “phytoplankton” referred to the 63–200 μm fractions which mainly represented micro-phytoplankton. Zooplankton was sampled with zooplankton triple nets (>200 μm) towed vertically (1 m sec^{-1}) in the entire water column.

Diet and stable isotope analyses

Stomachs were defrosted, weighed and fixed in 70% ethanol. Empty stomachs were counted and only used to calculate vacuity index (empty stomachs / empty stomachs + stomachs with food) or repletion index ($1 - \text{vacuity index}$) (Table 1). Prey in stomachs were sorted, identified to the lowest taxonomic level possible, counted, measured in mm T_L and weighed (dry weight to the nearest 0.01 mg recorded after 24 to 48 h at 60°C , depending on the prey-type) individually or by broader taxonomic groups. Otoliths of fish prey were measured in mm. Fish size vs otolith-size was calculated for each fish prey and used to estimate the T_L of fish prey partly digested, and then a dry weight correction was made. The relative contribution in dry weight (W%, Hyslop 1980) of each dietary category (W_d) to the total dry weight of all prey categories (W_{dTOT}) in the diet was used to describe hake feeding variations: $W (\%) = [W_d / W_{\text{dTOT}}] * 100$. This index was chosen, as weight is the best proxy of the energy provided by a prey to a predator (Tyler 1972).

Stable isotope analyses (SIA) were conducted on two sub-samples of surface POM and the 63- to 200- μm -sized fraction. One sub-sample was analysed without any prior treatment for $\delta^{15}\text{N}$ determination. The other, used for $\delta^{13}\text{C}$ analysis, was acidified with 1% HCl solution to remove carbonates, rinsed with distilled water and oven-dried at 40°C for 24 h, as carbonates have a higher $\delta^{13}\text{C}$ than organic carbon (DeNiro and Epstein 1978, Lorrain et al. 2003). SIA on fish and crustaceans were conducted on the same samples as those for stomach analysis between 2004 and 2006. Samples of muscle posterior to the head for fish, of caudal muscle for shrimp and of whole organisms for zooplankton and suprabenthos were used for SIA. Muscle samples were oven-dried and ground into a powder with a mortar and pestle. Crustaceans were decalcified and samples were divided into two sub-samples and treated as surface POM. Samples of large crustaceans and fish were analysed individually, whereas samples of small crustaceans were pooled to obtain enough material for analysis. Powdered samples were weighed (~1 mg) into tin capsules and combusted in a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Mylnefield Research Services-SCRI, Scrimgeour and Robinson 2003). Based on standard deviation of within-run replicate measurements of standards, analytical error was estimated to be $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements. Stable isotope values are expressed in the standard δ -notation as parts per thousand (‰) relative to Vienna Pee Dee Belemnite ($\delta^{13}\text{C}$) and atmospheric air ($\delta^{15}\text{N}$) standards. SIA were limited to the prey size range consumed by hake. When a large prey size range was consumed, different length-categories were considered.

Lipids were not extracted from our samples prior to SIA. The mean level of lipids (%) in muscle measured over 64 individuals (5–71 cm) was estimated to $5.17\% \pm 2.67\%$. This mean value close to 5% can be considered as a low lipid concentration inducing no bias on $\delta^{13}\text{C}$ values (Post et al. 2007).

The hake trophic foodweb was established from the mean ($\pm\text{SE}$) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of hake and its different prey only for the year 2005 because it was the most complete year for isotopic data (Table 2). Two main sources of organic matter, the marine phytoplankton and the Rhône River POM, were identified in this area.

Statistical analyses

To evaluate ontogenetic changes in hake diet composition, a hierarchical agglomerative cluster analysis was performed on the dry weight percentages (W%) of each dietary category of each size class (using Euclidean distance and Ward's minimum-variance method). Hake were grouped by 2-cm T_L class until 24 cm and by 5-cm T_L class afterwards. The spatial and temporal variations in hake diet were examined by comparing W% of each prey category in the resulting length groups defined by the cluster analysis.

To study the relationship between the ontogenetic changes in prey size and hake size, we used simple linear regression analysis, and we used quantile regres-

Table 1. – Diet composition of hake according to size (total length, cm) from the GoL in 2004-2006, expressed as percentage by dry weight of each prey category (W%). Total number of stomachs included stomachs with and without food, stomachs regurgitated, and stomachs not found because they were eaten by necrophages during the catch. (*, values <0.1%; -, prey category not found). Unid., unidentified.

Total length (cm)	05-06	07-14	15-24	25-39	40-49	50-74	TOT
Stomachs with food	75	655	631	449	160	31	2001
Empty stomachs	23	306	450	275	171	49	1274
Everted/not found stomachs	13	101	41	77	144	38	414
Total number (n)	111	1062	1122	801	475	118	3689
Vacuity index (%)	23	32	42	38	52	61	
Feeding intensity (%)	77	68	58	62	48	39	
Number of food types	10	32	21	16	21	11	
CRUSTACEANS	94.5	16.6	0.8	0.6	0.6	0.7	
Amphipoda							
<i>Ampelisca</i> sp.	-	2.3	-	-	-	-	
<i>Vibilia armata</i>	-	0.3	-	-	-	-	
<i>Vibilia</i> sp.	-	0.2	-	-	-	-	
Amphipoda Unid.	71.9	1.9	*	*	-	-	
Cumacea							
Cumacea Unid.	1.4	*	*	-	-	-	
Euphausiacea							
Euphausiacea Unid.	-	0.6	-	-	-	-	
Mysidacea							
<i>Leptomysis</i> sp.	2.1	1.0	-	-	-	-	
Mysidacea Unid.	6.2	0.8	-	-	-	-	
Natantia							
Alpheidae Unid.	-	0.2	*	*	*	*	
<i>Alpheus glaber</i>	-	0.2	*	*	*	-	
<i>Alpheus</i> sp.	-	*	*	*	*	-	
Caridea Unid.	-	-	0.2	*	*	-	
Natantia Unid.	5.5	3.5	0.4	0.3	0.2	0.1	
<i>Pasiphaea sivado</i>	-	-	-	-	-	*	
Penaeidae Unid.	-	0.2	-	-	-	-	
<i>Philocheira</i> sp.	4.8	3.0	*	-	-	-	
<i>Plesionika</i> sp.	-	-	-	-	0.1	-	
<i>Processa canaliculata</i>	-	0.1	*	*	-	-	
<i>Processa</i> sp.	0.7	0.2	*	*	*	-	
Processidae Unid.	2.1	1.3	*	-	-	-	
<i>Solenocera membranacea</i>	-	*	*	0.3	0.2	0.6	
Solenoceridae Unid.	-	-	-	*	-	-	
Reptantia							
<i>Liocarcinus depurator</i>	-	-	-	*	*	-	
Suprabenthos Unid.	-	0.5	0.1	-	-	-	
Crustacea Unid.	-	0.2	*	*	0.1	-	
FISH	5.5	82.1	98.1	98.8	98.6	99.2	
Benthic fish	5.5	15.0	2.1	0.8	6.8	5.7	
Callionymidae Unid.	-	0.3	-	-	-	-	
<i>Conger conger</i>	-	-	0.2	*	0.6	-	
<i>Deltentosteus quadrimaculatus</i>	-	-	0.1	*	*	-	
Gobiidae Unid.	1.4	1.1	*	*	*	-	
<i>Gobius niger</i>	-	1.5	0.6	-	0.1	-	
<i>Lepidopus caudatus</i>	-	-	-	-	4.2	-	
<i>Lepidotrigla cavillone</i>	-	-	-	0.2	-	-	
<i>Lesueurigobius friesii</i>	4.1	11.1	1.1	*	*	-	
<i>Mullus</i> sp.	-	-	0.2	*	-	-	
<i>Phycis blennoides</i>	-	-	-	-	1.8	5.7	
<i>Phycis</i> sp.	-	-	-	0.7	-	-	
Triglidae Unid.	-	1.0	-	-	-	-	
Demersal fish	-	18.8	2.9	3.8	12.8	21.3	
<i>Argentina sphyraena</i>	-	-	-	1.3	0.1	-	
<i>Capros aper</i>	-	-	-	-	0.7	3.5	
<i>Cepola macrophthalmia</i>	-	-	0.9	0.6	2.8	10.0	
<i>Epigonus denticulatus</i>	-	-	-	0.2	-	-	
<i>Gaidropsaurus biscayensis</i>	-	0.7	-	-	-	-	
<i>Merluccius merluccius</i>	-	3.4	0.6	0.1	1.1	4.1	
<i>Trisopterus minutus</i>	-	14.8	14	1.5	8.1	3.7	
Pelagic fish	-	43.6	79.1	88.2	75.7	28.1	
<i>Engraulis encrasicolus</i>	-	9.8	30.4	5.7	2.8	-	
<i>Micromesistius poutassou</i>	-	2.7	1.4	2.8	29.8	25.7	
<i>Sardina pilchardus</i>	-	21.6	38.7	74.1	38.3	-	
<i>Scomber scombrus</i>	-	-	0.3	0.7	0.5	-	
<i>Sprattus sprattus</i>	-	-	0.2	-	-	-	
<i>Trachurus mediterraneus</i>	-	-	0.1	-	-	-	
<i>Trachurus</i> sp.	-	-	*	0.1	0.6	1.6	
Pelagic fish Unid.	-	9.5	8.0	4.9	3.8	0.8	
Fish Unid.	-	4.6	14.0	5.9	3.3	44.1	
CEPHALOPODS	-	1.0	0.5	-	0.4	-	
<i>Alloteuthis</i> sp.	-	0.8	0.1	-	-	-	
<i>Sepioida</i> sp.	-	0.2	0.3	*	-	-	
Teuthida Unid.	-	-	-	*	*	-	
Cephalopods Unid.	-	*	*	*	0.4	-	

Table 2. – Number of $\delta^{15}\text{N}$ samples per hake size class, year and season.

Hake size classes	2004		2005		2006	
	spring	autumn	spring	autumn	spring	autumn
5-6	11	2	8	–	–	–
7-14	49	37	32	23	–	–
15-24	–	10	8	10	–	–
17-25	34	30	32	30	–	–
25-39	65	51	98	78	–	13
40-49	29	14	37	20	–	74
50-74	19	3	9	5	–	61

sions to estimate changes in minimum and maximum prey size. Quantiles ranged between the 90th and 99th for upper bound and the 1st and 10th for the lower bound.

We also investigated variations in hake $\delta^{15}\text{N}$ based on all available isotopic data (2004-2006) and tested the potential influence of different factors (season, depth, east-west gradient, sex) and continuous variables (length, condition, $\delta^{13}\text{C}$) as well as potential interactions between these explanatory variables, using generalized linear models (Venables and Dichmont 2004). Because the adults and the juveniles are not sympatric and because juveniles were not collected on the shelf-break and the upper-slope (Fig. 2), we performed one model for the juveniles and another for the adults. Both models included all factors and variables, but sex was added as a supplementary factor for the model on adults. Interactions between factors and variables were also tested and presented only when significant. As $\delta^{15}\text{N}$ is a continuous positive variable that is not normally distributed, we chose a Gamma error distribution with an identity link function. Diagnostic plots including the predicted values of mean of response and the standardized Pearson residuals, as well as the correlation among parameters, were examined for each analysis performed. The Akaike information criterion (AIC) was used to select the final model.

Hake maturity was identified according to two categories: juvenile or adult. Fish were considered as juvenile when the attributed maturity stage was virgin or at the beginning of maturation. Male adult stages were defined from the maturity scale used during the MEDITS surveys (Anon., 2013). Female adult stages were defined from gonadosomatic index (GSI) calculated as $\text{GSI}=100(\text{GW}/\text{W})$, where GW is the gonad wet weight and W is the observed individual eviscerated weight.

Fish condition was estimated by the relative condition factor, Kn , proposed by Le Cren (1951, see also Froese 2006) computed as $\text{Kn}=\text{W}/\text{aL}^n$, where W is the observed individual eviscerated weight, L is the T_L in cm, and aL^n is the estimated eviscerated weight from the $\log_{10} \text{W}-\log_{10} \text{L}$ relationship, where: $\text{aL}^n=10^{-\text{intercept}+\text{slope} \cdot \log_{10} \text{L}}$. In the original formula, W was the total weight of the fish, but we considered the eviscerated weight for two reasons: (i) the weight of stomach content is highly variable and can therefore bias the estimation of the relation aL^n ; and (ii) the condition is here used as an explanatory variable of $\delta^{15}\text{N}$ in hake muscle.

Statistical analyses were performed with the support of SPSS 17 (SPSS 2008) and R Softwares (R Development Core Team 2009).

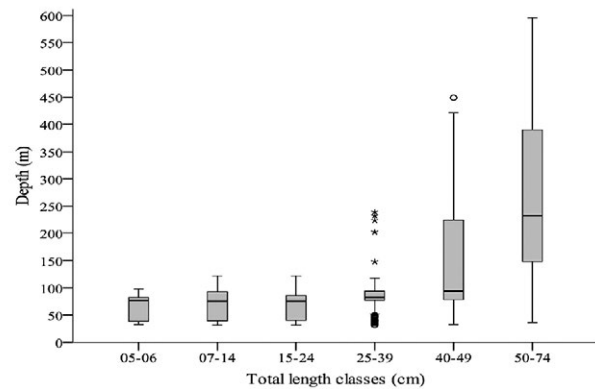


Fig. 2. – Spatial distribution of the samples of hake in the GoL in 2004-2006 (n=2483, min depth=31 m, max depth=596 m).

RESULTS

Hake diet

Among the 3689 hake sampled, 2001 showed stomachs with food, 1274 empty stomachs (39%) and 414 stomachs regurgitated or not found because they were eaten by necrophages. The vacuity index increased with length (23% to 61%, Table 1). Larger individuals that displayed empty stomachs more frequently (61%) were caught in deeper waters (down to 600 m, Fig. 2). Fish contribution in hake diet increased with hake length from 5.5% to 99.2% (Table 1). Crustaceans were the dominant food in the smallest individuals and cephalopods never exceeded 1%. The results of cluster analysis clearly differentiated six groups of diet size classes (Fig. 3), confirming the changes in hake diet during its growth. The smallest size class (5-6 cm T_L , a singleton) included a low number of prey types (10), mostly crustaceans (94.5%) with a high contribution of amphipods (71.9%). By contrast, the second smallest group in size (7-14 cm T_L) displayed the most diversified diet (32 prey types). Benthic and demersal fish species were nearly as important (33.8%) as pelagic fishes (43.6%), while crustaceans were clearly less important (16.6%). The following groups (hake of 15-24, 25-39 and 40-49

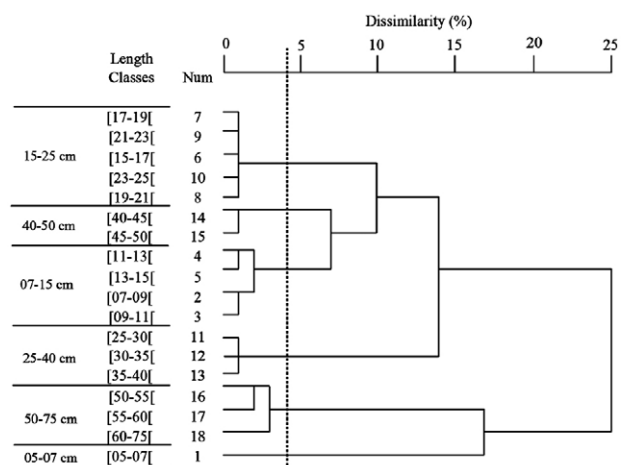


Fig. 3. – Dendrogram representing hake dietary similarity according to size classes, on the basis of mean percentage contribution (Cp: W%) of each food category.

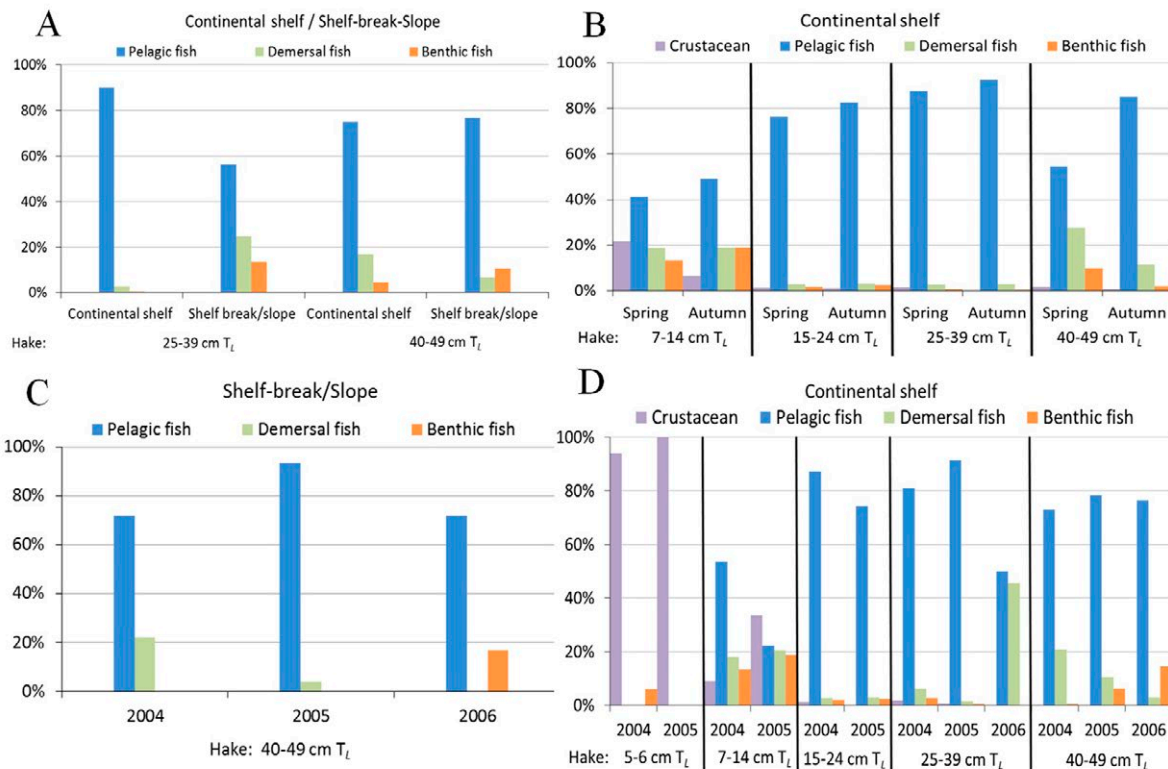


Fig. 4. – Spatio-temporal feeding variations of main prey groups according to (A) depth, (B) season, (C-D) year.

cm T_L) exhibited 16 to 21 prey types, including mostly fish (>98%), mostly pelagic species (75.7-88.2%). In the largest group (50-74 cm), the number of prey types decreased to 11 (similar to the smallest fish group) and the diet was mostly composed of fish (99.2%), among which 28.1% were pelagic, 21.3% demersal and 5.7% benthic (the remaining part of the fish diet could not be determined).

Only three pelagic fish, sardine (*Sardina pilchardus* Walbaum, 1792), European anchovy (*Engraulis encrasicolus* Linnaeus, 1758) and small blue whiting (*Micromesistius poutassou* Risso 1827), two demersal fish, poor cod (*Trisopterus minutus* Linnaeus, 1758) and red bandfish (*Cepola macrophthalma* Linnaeus, 1758), and two benthic fish, *Lesueurigobius friesii* (Malm, 1874), and the greater forkbeard (*Phycis blennoides* Brünnich, 1768), exceeded individually more than 5% of dry weight of hake diet (Table 1). The contribution of the three main pelagic fish species varied with hake length (Table 1). Sardine predominated in hake ranging from 7 to 49 cm T_L (21-74%), while anchovy only prevailed in the 15-24 cm T_L size class (30%) and small blue whiting in fish larger than 39 cm T_L (26-30%). The other groups never exceeded 15%. Cannibalism was observed in all size classes displaying a piscivorous diet, but remained low (0.1 to 4.1%). It was higher in the smallest size class (3.4%) and in the largest hake (4.1%), with a maximum rate on the slope (6%).

Spatio-temporal feeding variations

Because all hake size classes did not occur in all depth ranges, seasons and years, the influence of these

factors on hake diet were examined with separate data sets (Fig. 4A-D).

The effect of depth (continental shelf vs shelf-break/slope) on the diet was analysed on 25-49 cm T_L (2 size classes) (Fig. 4A). In the first size class (25-39 cm T_L), pelagic fish was the main prey (90%) on the continental shelf, while hake consumed 2/3 pelagic fish and 1/3 demersal or benthic fish on the shelf-break/slope. Sardine was the main prey on the continental shelf (77%), while small blue whiting dominated on the shelf-break/slope (42%). In the second size class (40-49 cm T_L), there was no difference in the proportion of pelagic fish or in the proportion of demersal or benthic fish between the two areas. Nonetheless, sardine also dominated hake diet on the continental shelf (63%), while small blue whiting dominated in deeper waters (74%).

The analysis of dietary changes with season (spring vs autumn) was only possible on the continental shelf for 7-49 cm T_L (4 size classes) (Fig. 4B). Considering pelagic fish, there was no significant difference between seasons in the first three size classes (7-14 cm, 15-24 cm and 25-39 cm T_L), but the proportion of pelagic fish was 30% lower in spring than in autumn in the largest size class (40-49 cm T_L). Crustaceans were only preyed on by the 7-14 cm T_L class, especially in spring. Total fish prey represented 73% in spring and 87% in autumn in this size class. Demersal or benthic fish dominated more in spring (37%) than in autumn (13%) in the 40-49 cm T_L class.

Year-to-year variations were analysed separately on the shelf-break/slope in only one size class (40-49 cm T_L) and on the continental shelf (5-49 cm T_L) in 5 size classes (Fig. 4C-D). On the shelf-break/slope

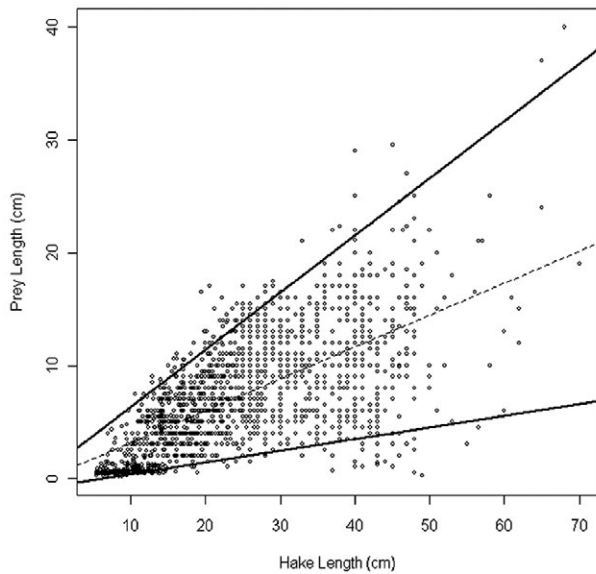


Fig. 5. – Hake size–prey size scatter diagram. Ontogenetic changes in prey sizes consumed with increasing hake size for all prey combined. Continuous lines, minimum (5th quantile) and maximum (95th quantile) prey sizes estimated by quantile regression; dashed line, mean prey sizes estimated by least-square regression; $n=1702$.

(Fig. 4C), where small blue whiting largely dominated (>70% the pelagic fish group in the diet of the 40–49 cm T_L class, there was no difference between 2004 and 2006 in the proportion of pelagic fish (72%) or demersal/benthic fish (20%). On the continental shelf (Fig. 4D), there were no major differences between years in the respective proportion of pelagic fish, demersal fish and crustaceans, except in the 7–14 cm and the 25–39 cm T_L classes. In the 7–14 cm T_L class, the proportion of small pelagics (54%) dominated in 2004 and the proportion of crustaceans (33%) increased in 2005. In the 25–39 cm T_L class, the proportions of small pelagics represented more than 80% in 2004 and 2005, but only 50% in 2006. Yearly diet changes were mainly observed at the level of the dominant crustaceans in the smallest size classes (5–6 cm T_L): amphipods dominated in 2004 (78%), whereas natantia decapods (55%) and mysids (45%) prevailed in 2005.

Prey–predator length relationships

The range of prey sizes consumed by hake increased significantly with increasing fish size ($R^2=0.653$, $N=1702$, $P<0.0001$, Fig. 5). The slopes of the extreme bounds (5th–95th quantiles) of prey size distribution were also significant ($P<0.0001$), but of a different amplitude (the slope was higher for the 95th quantile than for the 5th one, Fig. 5). Hake 5–6 cm T_L class fed on a mean length prey of 0.7 ± 0.05 cm T_L and the following

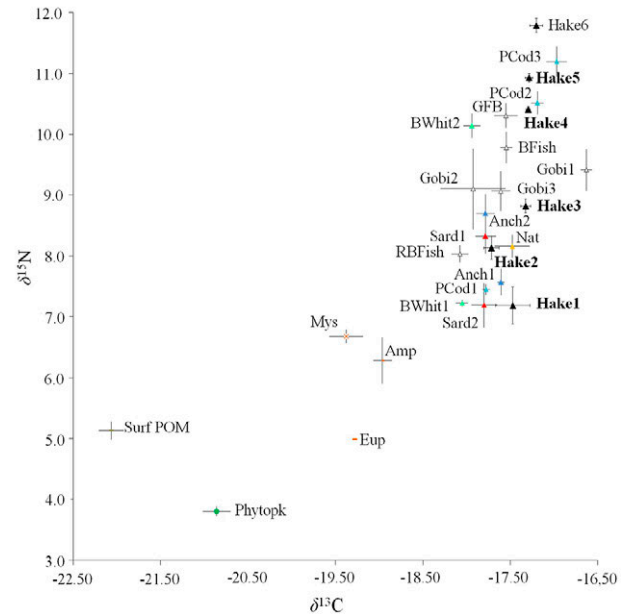


Fig. 6. – Mean (\pm SE) values of $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) for main prey of hake trophic web in the GoL in 2005. Codes: Surf POM, Surface Particulate Organic Matter; Phytoplank, Phytoplankton; Zoopl, Zooplankton; Amp, Amphipods; Eup, Euphausiids; Mys, Mysids; Nat, Natantia; Hake1, Hake 5–6 cm; Hake2, Hake 7–14 cm; Hake3, Hake 15–24 cm; Hake4, Hake 25–39 cm; Hake5, Hake 40–49 cm; Hake6, Hake 50–74 cm; Gob1, *Delentosteus quadrimaculatus*; Gob2, *Gobius niger*; Gob3, *Lesueurigobius friesii*; GFB, Greater Forkbeard; BFish, Boar Fish; RBFish, Red Bandfish; Sard1, Sardine <13.5 cm; Sard2, Sardine ≥ 13.5 cm; Anch1, Anchovy <14 cm; Anch2, Anchovy ≥ 14 cm; BWhit1=Blue Whiting <15 cm; BWhit2, Blue Whiting ≥ 15 cm; PCod1, Poor Cod ≤ 7 cm; PCod2, Poor Cod 8–13 cm; PCod3, Poor Cod ≥ 14 cm.

size classes fed on 2.6 ± 0.1 cm, 6.6 ± 0.15 cm, 9.9 ± 0.15 cm, 11.4 ± 0.4 cm and 15.2 ± 1.7 cm T_L , respectively. However, hake was able to ingest larger prey, $\geq 2/3$ of its body size in the case of the red bandfish (*C. macrophthalma*). Hake size classes fed on different mean lengths of the main fish prey such as gobids, anchovy, sardine, blue whiting and poor cod (Table 3).

Hake trophic web

The hake trophic web was based on a marine phytoplankton source and represented a continuum of feeding types ranging from crustaceans to pelagic, benthic and demersal fish (Fig. 6). As expected, phytoplankton and suprabenthic crustaceans (amphipods, euphausiids, and mysids) displayed the lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Stable isotope ratios of the main prey types of hake ranged from 5‰ to 11.2‰ for $\delta^{15}\text{N}$ and from -20.3 ‰ to -16.9 ‰ for $\delta^{13}\text{C}$ (Table 4). The smallest size classes of fish prey displayed a lower $\delta^{15}\text{N}$ value than the largest ones, except for sardine. The largest sardine (≥ 13.5

Table 3. – Mean size \pm SE of the main fish prey eaten per hake size class.

Hake size classes (cm)	Gobid sp.	Anchovy	Sardine	Blue whiting	Poor cod
7–14	3.9 ± 0.2	6.6 ± 0.4	5.8 ± 0.3	7.5 ± 0.3	5.5 ± 0.3
15–24	4.7 ± 0.4	9.0 ± 0.2	8.1 ± 0.3	10.8 ± 1.4	6.5 ± 0.5
25–39	5.1 ± 0.6	9.0 ± 0.4	12.7 ± 0.2	11.3 ± 0.9	8.7 ± 0.8
40–49	6.0 ± 1.2	8.1 ± 1.0	13.3 ± 0.4	14.7 ± 0.7	11.8 ± 1.2
50–74				18.6 ± 1.4	16.5

Table 4. – Mean isotopic signature with standard error (SE) by size class (SC) in the GoL in 2005.

	SC (cm)	Code	n	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)	
				mean	SE	mean	SE
Surface Particulate Organic Matter		Surf POM	55	5.13	0.15	-22.07	0.14
Phytoplankton.		Phytopk	24	3.80	0.08	-20.86	0.16
Zooplankton		Zoopk	6	6.71	0.63	-21.41	0.31
Amphipods		Amp	9	6.28	0.38	-20.34	0.11
Euphausiids		Eup	3	4.99	0.03	-19.96	0.02
Mysids		Mys	9	6.68	0.11	-20.34	0.19
Natantia		Nat	41	8.16	0.19	-17.90	0.20
<i>Delientosteus quadrimaculatus</i>	8	Gob1	19	9.41	0.34	-16.92	0.06
<i>Gobius niger</i>	11	Gob2	16	9.10	0.66	-18.12	0.37
<i>Lesueurigobius friesii</i>	6.4	Gob3	29	9.06	0.32	-17.87	0.11
<i>Phycis blennoides</i>	15.7	GFHake	6	10.31	0.20	-17.55	0.13
<i>Capros aper</i>	13	BFish	8	9.78	0.26	-17.82	0.07
<i>Cepola macrophthalma</i>	25.8	RBFish	15	8.05	0.15	-18.41	0.06
<i>Sardina pilchardus</i>	<13.5	Sard1	19	8.32	0.28	-18.08	0.12
<i>Sardina pilchardus</i>	≥13.5	Sard2	28	7.19	0.36	-18.74	0.15
<i>Engraulis encrasicolus</i>	<14	Anch1	39	7.57	0.22	-17.84	0.04
<i>Engraulis encrasicolus</i>	≥14	Anch2	10	8.70	0.32	-18.09	0.10
<i>Micromesistius poutassou</i>	<15	BWhit1	28	7.22	0.05	-18.28	0.07
<i>Micromesistius poutassou</i>	≥15	BWhit2	19	10.14	0.20	-17.93	0.10
<i>Trisopterus minutus</i>	≤7	PCod1	11	7.45	0.09	-17.99	0.04
<i>Trisopterus minutus</i>	8-13	PCod2	40	10.51	0.19	-17.36	0.07
<i>Trisopterus minutus</i>	≥14	PCod3	24	11.19	0.25	-17.11	0.12
<i>Merluccius merluccius</i>	5-6	Hake1	8	7.19	0.30	-17.67	0.20
<i>Merluccius merluccius</i>	7-14	Hake2	55	8.13	0.19	-17.85	0.09
<i>Merluccius merluccius</i>	15-24	Hake3	80	8.82	0.11	-17.45	0.06
<i>Merluccius merluccius</i>	25-39	Hake4	176	10.41	0.05	-17.44	0.02
<i>Merluccius merluccius</i>	40-49	Hake5	57	10.93	0.07	-17.44	0.04
<i>Merluccius merluccius</i>	50-74	Hake6	14	11.79	0.12	-17.32	0.07

Table 5. – Stepwise generalized linear model for factors and continuous variables controlling $\delta^{15}\text{N}$ variability in juvenile (A) and adult (B) hakes in the GoL. Parameter estimates (c) and standard error for the best fitting GLMs model.

Factors and continuous variables added	c	SE	Residual df	Deviance	Df	Deviance decrement	Cumulative deviance explained	% of total deviance explained	P-value (chi-squared)	AIC
A: Juvenile										
Intercept	5.056	.1893	497	12.407						1798
+ Length	.127	.0035	496	6.194	1	6.213	50.077	65%	0.000	1453
+ Season	2.678	.1387	495	4.579	1	1.615	63.093	17%	0.000	1305
+ Season*Length	-.073	.0060	494	3.160	1	1.419	74.531	15%	0.000	1122
+ Depth			492	2.850	2	0.310	77.029	3%	0.000	1074
+ E-W gradient	.217	.0626	491	2.783	1	0.067	77.569	1%	0.001	1064
B: Adult										
Intercept	7.132	.3442	334	1.197						648
+ Length	.061	.0042	333	0.931	1	0.266	22.222	44%	0.000	566
+ Season	-.461	.0551	332	0.777	1	0.154	35.087	25%	0.000	507
+ Depth	.449	.0789	331	0.693	1	0.084	42.105	14%	0.000	471
+ Sex	-.404	.0654	330	0.621	1	0.072	48.120	12%	0.000	436
+ Condition	1.086	.3214	329	0.601	1	0.02	49.791	3%	0.001	427
+ E-W gradient	.143	.0511	328	0.587	1	0.014	50.960	2%	0.005	422

cm T_L) displayed the most depleted $\delta^{13}\text{C}$ signature, just above phytoplankton and the suprabenthic crustaceans, which probably represented a large part of their diet. The lowest $\delta^{15}\text{N}$ values (7.2‰) were found in the largest sardine (≥13.5 cm T_L), in the smallest blue whiting (<15 cm T_L) and in the smallest hake (5-6 cm T_L). The small anchovy and poor cod showed slightly higher $\delta^{15}\text{N}$ values (7.5‰-8‰), followed by large anchovy, small sardine, red bandfish and hake 7-24 cm T_L class (8‰-9‰), and then by gobiids and boarfish (*Capros aper* Linnaeus, 1758) (9-10‰). Finally, the largest blue whiting (≥15 cm T_L), poor cod (≥8 cm T_L), hake (≥25 cm T_L) and the greater forkbeard exhibited the highest $\delta^{15}\text{N}$ values (≥10‰). A continuous increase in $\delta^{15}\text{N}$ with length was thus observed in hake, from 7.2‰ to 11.8‰. A slight increase (0.4‰) in hake $\delta^{13}\text{C}$ with length occurred from the smallest (-17.7‰) to the largest individuals (-17.3‰).

Hake $\delta^{15}\text{N}$ variation

This analysis was based on 892 isotope samples. All factors (season, depth, E-W gradient), two continuous variables (size and $\delta^{13}\text{C}$) and one interaction (season-length) were highly significant ($P < 0.001$) in the selected model for juveniles, but $\delta^{13}\text{C}$ was finally removed because of high correlation with the intercept (Table 5A). The length factor showed the highest contribution to the total explained deviance (50%) of hake $\delta^{15}\text{N}$ variability, followed by season (13%), season-length interaction (11%), depth (2%) and E-W gradient (1%).

The model selected for adults was similar to that of juveniles, but it also included the condition and sex as significant covariates, while the length-season interaction did not appear to be significant (Table 5B). Length had again the greatest contribution to hake $\delta^{15}\text{N}$ vari-

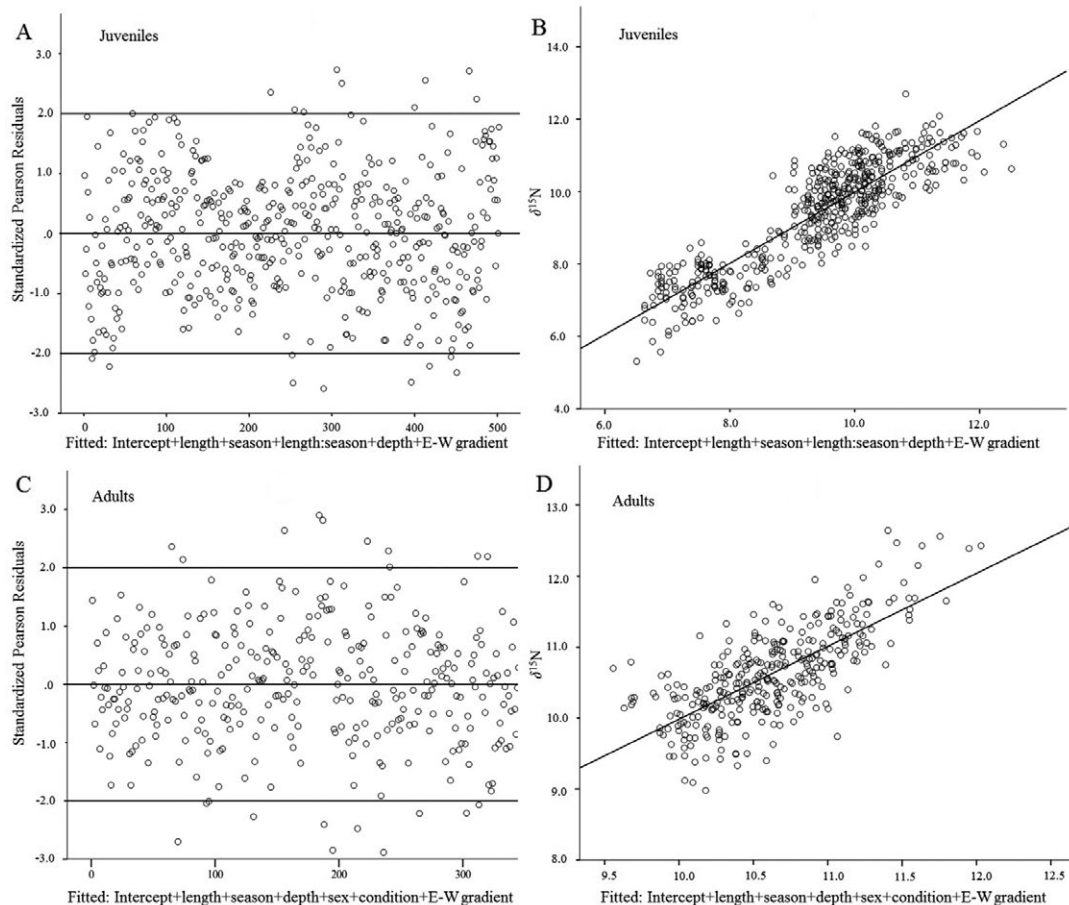


Fig. 7. – Results of the GLM with a Gamma error and an identity link for juvenile (A, B) and adult (C, D) hakes: plots of the residuals and the fitted values versus $\delta^{15}\text{N}$.

ability (22%), while season remained important (13%) and was followed by depth (7%), sex (6%), condition (2%) and E-W gradient (1%).

Juvenile and adult final models explained 77% and 51% of the total deviance, respectively. The diagnostic plots were satisfactory (Fig. 7A-D). Note that Figure 7B tends to show a lower number of data in the range of 8.0-10‰, which actually corresponds to a low sampling of individuals from 20 to 24 cm in comparison with the other size classes.

Both sexes exhibited a similar $\delta^{15}\text{N}$ trend with age but females had a higher $\delta^{15}\text{N}$ than males at the same age (Fig. 8A). The three smallest hake size classes (i.e. up to 24 cm T_L) displayed a lower $\delta^{15}\text{N}$ in spring than in autumn (Fig. 8B). This partially matched the seasonal variation of euphausiids $\delta^{15}\text{N}$ used as the primary consumer baseline, with higher values in autumn. From 25 cm T_L there were no such large seasonal differences in the $\delta^{15}\text{N}$. In spring, the first two size classes showed similar $\delta^{15}\text{N}$, whereas the third size class (15-24 cm T_L) displayed an intermediate $\delta^{15}\text{N}$ value between juveniles (<15 cm T_L) and specimens larger than 24 cm T_L . In autumn, $\delta^{15}\text{N}$ increased regularly between the different size classes. In the largest hakes (25-75 cm T_L), the trends of $\delta^{15}\text{N}$ were similar in both seasons. Higher $\delta^{15}\text{N}$ values in hake ≥ 25 cm T_L were observed on the continental shelf than on the shelf-break/slope (Fig. 8C).

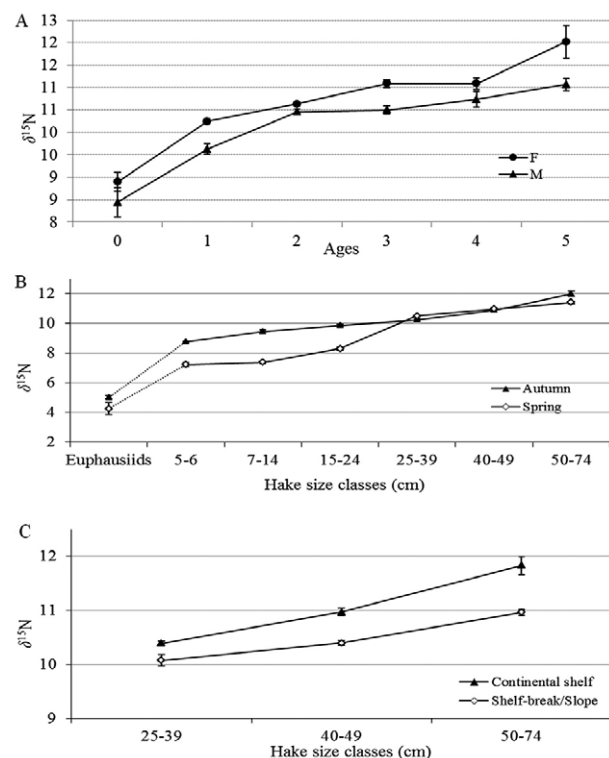


Fig. 8. – Ontogenetic $\delta^{15}\text{N}$ changes of hake with (A) sex (F, female; M, male), (B) season ($\delta^{15}\text{N}$ Euphausiids = baseline) and (C) depth.

DISCUSSION

Hake diet and feeding strategy

The results of this study confirm that hake is a carnivorous predator that feeds on a variety of benthic, demersal and pelagic prey on the continental shelf and slope. Suprabenthic crustaceans and pelagic fish, i.e. sardine, anchovy and small blue whiting, were the main components of the diet and cephalopods were of minor importance. Diet changes with increasing body length from crustacean to piscivorous regimes, as previously described in the GoL (Bozzano et al. 1997, Ferraton et al. 2007) and in different hake populations world-wide (e.g. Papaconstantinou and Caragitsou 1987, Payne et al. 1987, Du Buit 1996). The shift occurred progressively between 7 and 14 cm, reaching the piscivorous regime at 15 cm T_L before the end of the first year of life (Mellon-Duval et al. 2010). The main difference between regions is related to the dominant pelagic fish preyed on by hake: herring in the Pacific (Tanasichuk et al. 1991), anchovy and pilchard in South Africa (Pillar and Wilkinson 1995), horse mackerel and anchovy in the northern Bay of Biscay (Guichet 1995), and blue whiting and horse mackerel in the Cantabrian Sea (Velasco and Olaso 1998).

Cannibalism has been commonly observed in hake populations (Guichet 1995, Garrison and Link 2000, Cartes et al. 2004). It also occurred in the GoL, mostly on the shelf-break but at low levels (<5%), confirming previous findings by Bozzano et al. (1997) and similar results in the southern Bay of Biscay and Portuguese coasts (Velasco and Olaso 1998, Cabral and Murta 2002). This contrasts with the central Tyrrhenian Sea, the northern Bay of Biscay and the Celtic Sea, where cannibalism can exceed 15% (Mahe et al. 2007, Carpentieri et al. 2005). The low level of cannibalism in the GoL could be related to the weak overlap of small and large hakes, which mainly occurred during the reproductive period on the shelf-break.

Year-to-year (like seasonal) variations in diet were of low magnitude, except for the types of suprabenthic crustaceans preyed on by the smallest hake (5-6 cm). Amphipods were dominant in 2004 while mysids and shrimps were dominant in 2005. Similar variations were observed with a dominance of euphausiids and mysids in 2002 and of shrimps and amphipods in 2003 (Ferraton et al. 2007).

The present study confirms that hake is an opportunistic feeder, as already demonstrated (Bozzano et al. 1997, Hidalgo et al. 2008), but also shows that the length and the diversity of prey vary with hake size, probably as a result of different spatial distributions and/or foraging migration. Bozzano et al. (2005) pointed out that 2.5-4.5 cm T_L hake have not yet moved to the bottom and the 5-6 cm group represents the first recruits that settle. At this stage, juvenile hake has low mobility (Recasens et al. 1998, Arneri and Morales-Nin 2000) and our results indicate that their diet is restricted by mean prey size <1 cm T_L and low prey diversity. The maximum prey diversity observed in the following hake size-group (7-14 cm) is likely to be linked to the

mixed diet of crustaceans and fish and to the increasing mean length of prey to 2.6 cm T_L . This wider spectrum of prey leads us to postulate that foraging migrations could start at this size class, as corresponds to previous findings in the Tyrrhenian Sea (Bartolino et al. 2008). Increasing mobility is related to the development of sensory organs allowing hake to undertake vertical nocturnal migration in water columns in response to similar movement of their prey (Bozzano et al. 2005, Mas-Riera 1991, Lombarte and Popper 2004). The decrease in diversity and the increase in the range of prey size in the diet of the three following hake size classes, from 15 to 49 cm, is probably the result of a restrictive piscivorous regime and could suggest more mobility in the water column to catch larger fish prey.

Foodweb structure

The $\delta^{13}C$ values of different size classes exhibit little variation, indicating that the hake trophic web in the GoL is based mainly on a marine phytoplankton source (and not on a Rhône river discharge-related foodweb). By contrast, $\delta^{15}N$ values changed with body size and season for both juvenile and adult hake. Size and season interaction influenced $\delta^{15}N$ in juveniles, and depth and sex also affect $\delta^{15}N$ in adults. Because small crustaceans, mainly eaten by the smallest hake, were pooled to obtain enough material for analysis, the detail of isotopic results concerning this hake size may not be very fine.

The $\delta^{15}N$ variations in a consumer can be related to changes in $\delta^{15}N$ of the baseline or changes in its diet or growth (Olive et al. 2003, Trueman et al. 2005, Sweeting et al. 2007). In the present study, ontogenetic shift in the composition and size of the prey probably explains the bulk of variations in $\delta^{15}N$ observed. Because our work is based on only two sampling periods, it is not possible to determine a direct relationship between the composition of the diet and the isotopic signature. There is indeed a time lag between the ingestion of prey and its incorporation in the tissue of the predator, and a minimum of 4 to 6 sampling periods would have been necessary. Nonetheless, the increase of $\delta^{15}N$ with body length is commonly observed in many predatory fish species (Overman and Parrish 2001, Badalamenti et al. 2002, Jennings et al. 2002), including hake (Le Loc'h and Hily 2005). In our dataset, crustaceans had a lower $\delta^{15}N$ than fish, while large blue whiting, large demersal and benthic fish had a higher $\delta^{15}N$ than the main fish prey: sardine, anchovy and small blue whiting. Most fish prey, except sardine, increased in $\delta^{15}N$ with body length.

The differences observed between spring and autumn in the $\delta^{15}N$ baseline (euphausiids) may partially explain the $\delta^{15}N$ differences observed in juvenile hakes. A lower growth rate leads to lower consumption and higher excretion of nitrogen compounds, resulting in a ^{15}N increase in a consumer (Olive et al. 2003, Trueman et al. 2005, Sweeting et al. 2007). Morales-Nin and Moranta (2004) showed that the growth rate of juvenile hakes is lower in autumn than in spring. This finding suggests that growth could be a contributory

factor in explaining the seasonal effect on $\delta^{15}\text{N}$ observed in juvenile hake. An increase of $\delta^{15}\text{N}$ inversely with depth was observed in hake ≥ 25 cm in the GoL, a finding which is consistent with the work of Sherwood and Rose (2005). Influence of sex on $\delta^{15}\text{N}$ could be due to an indirect effect of growth dimorphism, male eating smaller prey sizes than females of the same age (lower $\delta^{15}\text{N}$ for males).

Stock status considerations with regard to diet

Hake and its main pelagic prey, except blue whiting, are important fishery resources in the GoL. Sardine and anchovy dominated on the continental shelf and more generally in the northwestern Mediterranean (Palomera et al. 2007), while blue whiting dominated offshore from the shelf-break. All the pelagic fish make up 40% to 80% of hake diet in the GoL, indicating their key trophic role. Since the late 2000s, the pelagic ecosystem of the GoL has shifted to a different regime, characterized by a low biomass of anchovy and sardine related to a slowdown in growth and a bad body condition (Van Beveren et al. 2014, Brosset et al. 2015). Therefore, the population fluctuations and the general “state of health” of these two species may adversely affect the diet, body condition and reproduction of their predators, and consequently reinforce the decline of hake, a species that is already severely overexploited (Jadaud et al. 2014).

Because of growth dimorphism observed in hake of the GoL (males are indeed significantly smaller than females from 2 to 3 years old, Mellon-Duval et al. 2010), males feed longer than females on smaller prey (i.e. sardine, anchovy), which they find in abundance on the continental shelf. For this reason, we hypothesize that the long and intensive exploitation on the continental shelf by trawlers, which led to the reduction of the abundance of large individuals (80% of hake total catch in weight and >97% in number composed of specimens ≤ 38 cm T_L , Jadaud et al. 2014) could affect males and females differently. An increase in the mortality of males could then explain the unbalanced sex ratio observed (80% female against 20% male at 38 cm T_L , Jadaud et al. 2014) in the hake population of the GoL.

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